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REPRODUCTIVE TACTICS AND FEMALE BODY SIZE IN THE GREEN LYNX SPIDER, *PEUCETIA VIRIDANS* (ARANEAE, OXYOPIDAE)

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ABSTRACT

Data collected on life history traits of *Peucetia viridans*, representing three generations, were analyzed. A total of 61 females and their clutches were examined to determine the following: female mass, female tibia length, clutch mass, clutch size, mean mass per young, egg sac mass, egg sac mass per young, and relative clutch mass (an estimate of reproductive effort). Clutch mass, clutch size and egg sac mass are strongly correlated with female mass. *Peucetia viridans* has the reproductive tactic of producing young of optimum size, with the number of young varying in response to environmental pressures that influence female size, thus producing optimal reproductive effort. Relative clutch mass is also optimized and apparently not influenced by the variation in female mass, clutch mass or size. Egg sac mass per young is similar in small clutches and large clutches. These findings are discussed in terms of the species' life history characteristics.

INTRODUCTION

Most information on reproductive tactics in spiders comes from literature dealing with spider taxonomy, where some observations of spider size (usually body length) and clutch size (number of eggs or young in an egg sac) have been reported (Bristowe 1939, Kaston 1948, Gertsch 1949). For *Peucetia viridans,* the green lynx spider, Brady (1964) gives the number of eggs from egg sacs taken from several geographical regions. There are very few studies that deal with the precise relationships between the size of female spiders, number and size of offspring, and estimates of reproductive effort.

Any reproductive event can be described in terms of a triumvirate: reproductive effort, expenditure of energy per progeny, and clutch size (Pianka, 1983). Though the concept of reproductive effort (the proportion of total energy allocated to a reproductive event) is very useful, it is often quite difficult to quantify. An operational estimate of reproductive effort that has been used is a ratio of clutch mass to female mass (Vitt and Congdon, 1978). This ratio, termed relative clutch mass, is used in this paper.

Though many authors have noticed the general trend that larger females produce larger clutches, few (Peterson 1950, Kessler 1973, Riechert and Tracy

1975, Eberhard 1979) have studied this relationship closely in spiders. Enders (1976) has shown, using published data from a variety of studies, that clutch size among species of spiders is positively correlated with length of female and that other life history traits (hunting manner, habitat selection) also appear to be related to clutch size. The energy content of spider eggs was studied by Anderson (1978). He included data on mass-specific energy content of *P. viridans* eggs from five clutches along with data from eleven other species. He discussed these data in relation to female mass and clutch mass and suggested that caution by used when selecting an estimator of reproductive effort.

Our three-year study of certain reproductive parameters of *Peucetia viridans* (Hentz) enables us to examine closely its reproductive tactics as they relate to the energetics associated with the reproductive biology of the species. We analyze the relationships between such parameters as clutch size, clutch mass, egg sac mass, mean egg mass, relative clutch mass, and female mass. We also examine how some parameters change significantly and others remain constant from one generation to the next.

STUDY AREA AND NATURAL HISTORY

Two study areas in east Texas were selected. One study area was an old field located 1.6 km northwest of the city of Whitehouse (Smith County) near the western edge of the Australoriparian Biotic Province. This 1.22 hectare field is surrounded by an Oak-Hickory-Pine Forest. In late summer and early fall the tallest herbaceous vegetation consists of composites (*Veronia* sp., *Lactuca* sp., *Ambrosia* sp.) and an euphorb (*Croton capitatus*), these being the most commonly encountered plants on which there are female *P. viridans* and their egg sacs. Samples were taken from this site in 1980 and 1981. The second study site was an old field very similar to the first, located approximately 11.2 km north-northeast of the first site, 0.8 km south of The University of Texas at Tyler. Samples were taken from this site in 1983.

The life history and phenology of *P. viridans* have been examined by Whitcomb, Hite and Eason (1966) and Turner (1979). In east Texas, there appears to be one reproductive period with a single clutch produced by a female between mid-September and late October. Though multiple clutches have been reported from other areas, none was observed during this study.

METHODS

Samples were taken from September 29 to October 12, 1980, and from September 17 to October 25, 1981, and on October 11, 1983. Twenty-one females with their corresponding egg sacs were taken in 1980, 14 were taken in 1981, and 26 were taken in 1983. The following information was determined for each specimen: female mass (mg) after egg sac construction, length of first tibia of female (mm), mass of egg sac (mg), mass of clutch (mg) and clutch size (number of eggs or juveniles). Relative clutch mass (RCM, clutch mass/female mass), mean mass of young (MMY, clutch mass/clutch size), and mean egg sac mass per young (MEY, egg sac mass/clutch size) were calculated.

These data were statistically examined using the computer-packaged Statistical Analysis System (Freund and Littell, 1981). The significance level chosen was $\alpha = 0.05$. In addition to basic descriptive statistics the following were used: Duncan multiple range test to compare sample statistics by year; correlation; general linear regression, with coefficient of determination and test for homogeneity of slopes used to compare certain parameters to female size.

RESULTS

Tables 1 and 2 summarize sample statistics for each of the three years by parameter and for parameter totals.

Female mass and female tibia length were significantly different by year; the largest females were taken in 1981. Because the coefficients of variation (C.V.) did not vary greatly from year to year, the female size differences by year appear to be real.

Average clutch mass in 1980 was not significantly different form the other two years, but clutch mass in 1981 was significantly different from that of 1983. Note that in 1980 the C.V. is large compared to the other two years. Clutch mass appears to vary more than female size. There is a significant positive correlation of clutch mass and female mass by year and for the data combined. When clutch mass is regressed against female mass (Figure 1), 55.14% of the total variation in clutch mass is explained by the linear relationship to female mass in 1980, 58.12% in 1981, 63.38% in 1983, and 66.53% for the data combined. Regression coefficients are not significantly different for these data.

Clutch sizes in years 1980 and 1983 were not significantly different from each other, but clutch size in 1981 was significantly different from that of the other

Table 1.—Means (standard errors) / ranges of reproductive parameters of *Peucetia viridans*. Statistics underlined are not significantly different by year (P>0.05).

Year	1980	1981	1983	Total
Sample	21	14	26	61
Female mass (mg)	106.12(4.81)	226.07(14.30)	155.51(7.38)	154.70(7.45)
Range	77.10-164.10	168.10-335.40	85.90-214.10	77.10-335.40
Female tibia length (mm)	6.89(0.16)	9.07(0.17)	7.63(0.15)	7.70(0.14)
Range	6.66-8.21	7.92-10.18	6.22-8.86	5.66-10.18
Clutch mass (mg)	147.94(14.46)	266.78(21.82)	193.65(13.75)	194.70(10.66)
Range	42.10-360.10	131.60-403.60	66.70-375.00	42.10-403.60
Clutch size	98.38(9.64)	169.86(12.40)	114.08(7.66)	121.48(6.42)
Range	29-242	90-240	42-183	29-242
Mean mass per young (mg)	1.5.(0.03)	1.56(0.03)	1.70(0.04)	1.60(0.02)
Range	1.29-1.72	1.44-1.76	1.31-2.25	1.29-2.25
Egg sac mass (mg)	5.71(0.43)	13.16(0.75)	7.32(0.46)	8.11(0.47)
Range	3.60-11.90	9.60-18.40	3.40-12.20	2.40-18.40
Relative clutch mass	1.31(0.11)	1.18(0.07)	1.23(0.06)	1.27(0.04)
Range	0.49-2.23	0.69-1.50	0.55-1.91	0.49-2.23
Egg sac mass per young (mg)	0.06(0.01)	0.08(0.01)	0.07(0.00)	0.07(0.00)
Range	0.03-0.12	0.05-0.13	0.04-0.09	0.03-0.13

Table 2.—Coefficients of variation (coefficients of determination) of reproductive parameters of *Peucetia viridans*. Statistics underlined are not significantly correlated to female mass (P>.05); *=Regression coefficients for these parameters against female mass are not significantly different by year when compared to regression line of total.

Year	1980	1981	1983	Total
Female mass	20.75	23.67	24.19	37.62
Female tibia length	10.75	6.96	9.94	14.09
Clutch mass	44.80(0.5514)	30.60(0.5812)	36.22(0.6338)	42.77(0.6653)*
Clutch size	44.91(0.5735)	27.32(0.5419)	34.26(0.6802)	41.25(0.6435)*
Mean mass per young	8.10(0.0001)	6.17(0.1868)	13.16(0.0022)	11.80(0.0129)*
Egg sac mass	34.33(0.1601)	21.31(0.0160)	32.43(0.6486)	45.44(0.5883)
Relative clutch mass	30.88(0.1071)	21.84(0.0003)	24.62(0.0249)	27.09(0.0403)*
Egg sac mass per young	36.77(0.1766)	29.68(0.3476)	20.03(0.0462)	30.35(0.0006)*

two years. Clutch size also appears to vary more than female size. Significant positive correlation occurs between female mass and clutch size by year and for the data combined. Coefficients of determination indicate that 57.35% of the variation in clutch size is explained by a linear relationship to female mass (Figure 2) in 1980, 54.19% in 1981, 67.02% in 1983 and 64.53% for the data combined. Regression coefficients are significantly different for these data.

Mean mass of young was significantly different only in 1983. The C.V.'s are very small when compared to the C.V.'s of other parameters. There is no significant correlation of mean mass of young and female mass for any year nor for the data totals; neither is there a difference in regression coefficients by year.

Egg sac mass was significantly different by year. It was not significantly correlated to female mass in 1980 and 1981, though data from 1983 and the combined data show a significant correlation between these two parameters. Figure 3 shows the best-fit linear relationship between egg sac mass and female mass, with very little of the variation in egg sac mass being explained by female mass in 1980 and 1981, 16.01% and 1.6% respectively. The coefficients of determination are 64.86% in 1983 and 58.85% for the data combined. Slopes by year are significantly different from the slope of the composite regression line.

Relative clutch mass is not significantly different when compared by year. There is no significant correlation with female mass, and regression coefficients are not significantly different by year.

Egg sac mass per young is significantly different from other years only in 1981. There is no significant correlation between egg sac mass per young and female mass, nor are there significant differences in regression coefficients by year.

DISCUSSION

The results suggest that an analysis from two perspectives would be useful. First we examine the life history parameters as they relate to individual phenotypes, i.e., the expression of the parameters and their interactions. Next we consider the broader implications of these individual reproductive tactics as they relate to the species' life history characteristics.

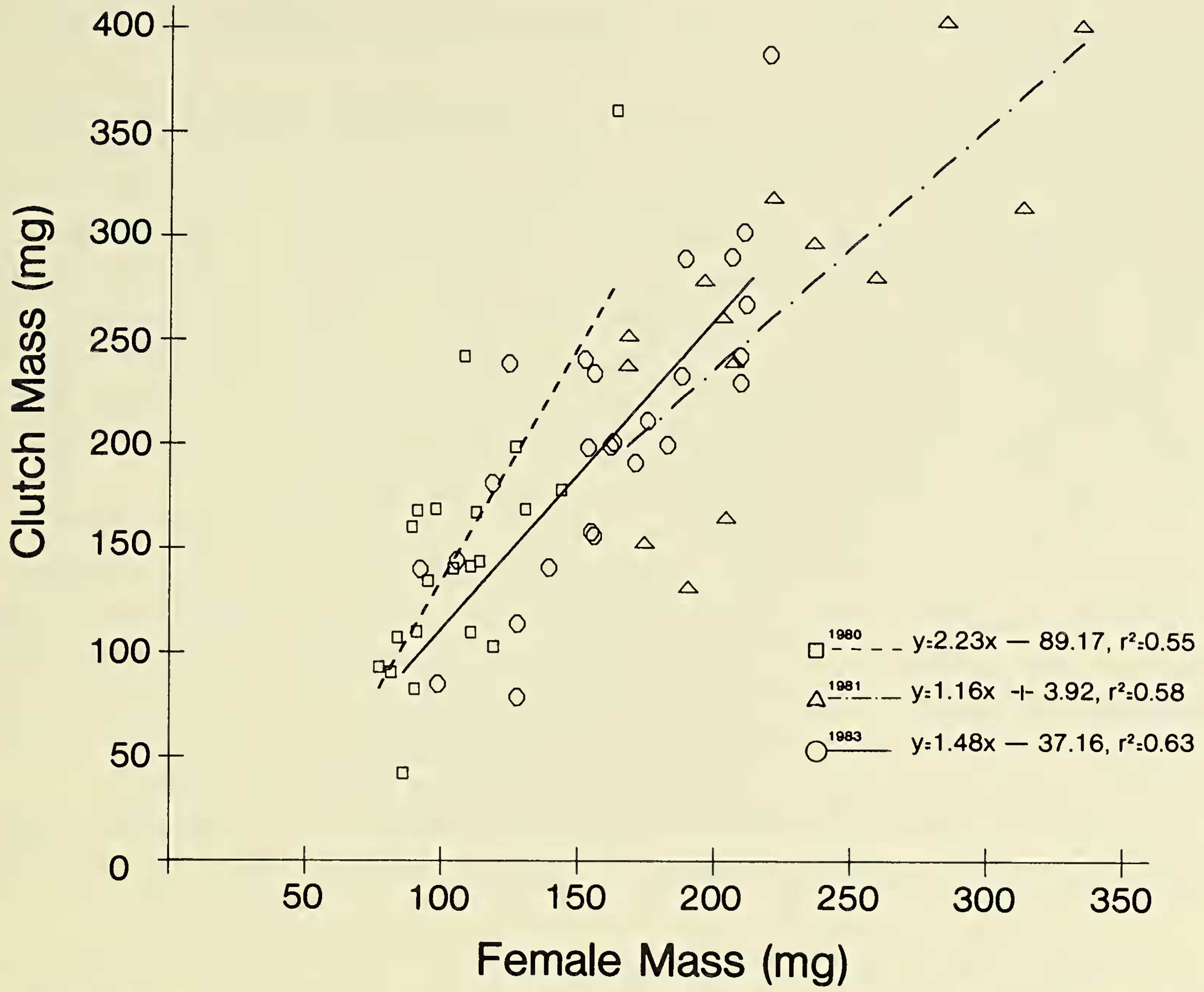

Fig. 1.—Regression of clutch mass against female mass of *Peucetia viridans* for three years. r^2 is the coefficient of determination.

It is clear that a reproductively successful female can vary greatly in size, the largest being some 4.4 times more massive than the smallest (Table 1). This allows for the exceptional range in clutch mass (42.10 - 403.60 mg) and clutch size (29 - 242) because these two parameters show high coefficients of determination when regressed against female mass (Figures 1 and 2). Although natural selection appears to favor individual variation in these three parameters, that variation does not affect reproductive effort. These data show that small females may have the same relative clutch mass as large females and that RCM does not change from one year to another (Table 1 and Table 2), implying an optimum RCM. This is striking, given that reproductive effort in some females is 4.5 times greater than in others. Since essentially none of this variation is explained by a linear relationship with female mass (or any other correlate of female mass) and since the two components of RCM covary so strongly, which would normally yield a constant RCM, we interpret the variation in RCM to be due to changes in female mass after oviposition. This effect is random in that, even though some females may have fed after oviposition, feeding frequency in the short time between oviposition and being collected is due to chance. This feeding effect is likely a minor component of variation in female mass, which is masked by the variation in female mass already existing at the time of oviposition. When the mass to mass ratio of RCM is calculated, the effect of variation due to post-oviposition feeding is exposed. We conclude that *P. viridans* has a reproductive tactic of optimal reproductive effort regardless of the variation present in female mass, clutch size and clutch mass.

Another parameter that is important in understanding reproductive tactics is the energy allocation per spiderling. We utilized mean mass of young to estimate this element. MMY is not correlated with any parameter discussed thus far. Natural selection appears to produce an optimum MMY; in two of the three years, it is the same. MMY also has the smallest C.V. of any parameter. This leads to the conclusion that *P. viridans,* rather than having small females reduce their allocation of energy per young so as to have more but smaller young, has a reproductive tactic to produce fewer young of optimum size. Larger females likewise produce young of optimum size, but more than them. This explains how both clutch size and mass are strongly correlated with female mass.

Our findings are in agreement with those of Anderson (1978), who found that variation in mass-specific energy content in spiders was less than variation in clutch size, and there was no correlation between energy content per unit egg mass and size of the female parent, egg size, or clutch size. In the light of these findings and those of our study, RCM appears to be a valid estimate of reproductive effort and may be a useful operational tool in studies that require an indirect measure of the energy partitioned to reproduction by spiders.

In spiders, another quantitative reproductive parameter is important, namely egg sac mass. This parameter varies in a manner similar to clutch size and mass.

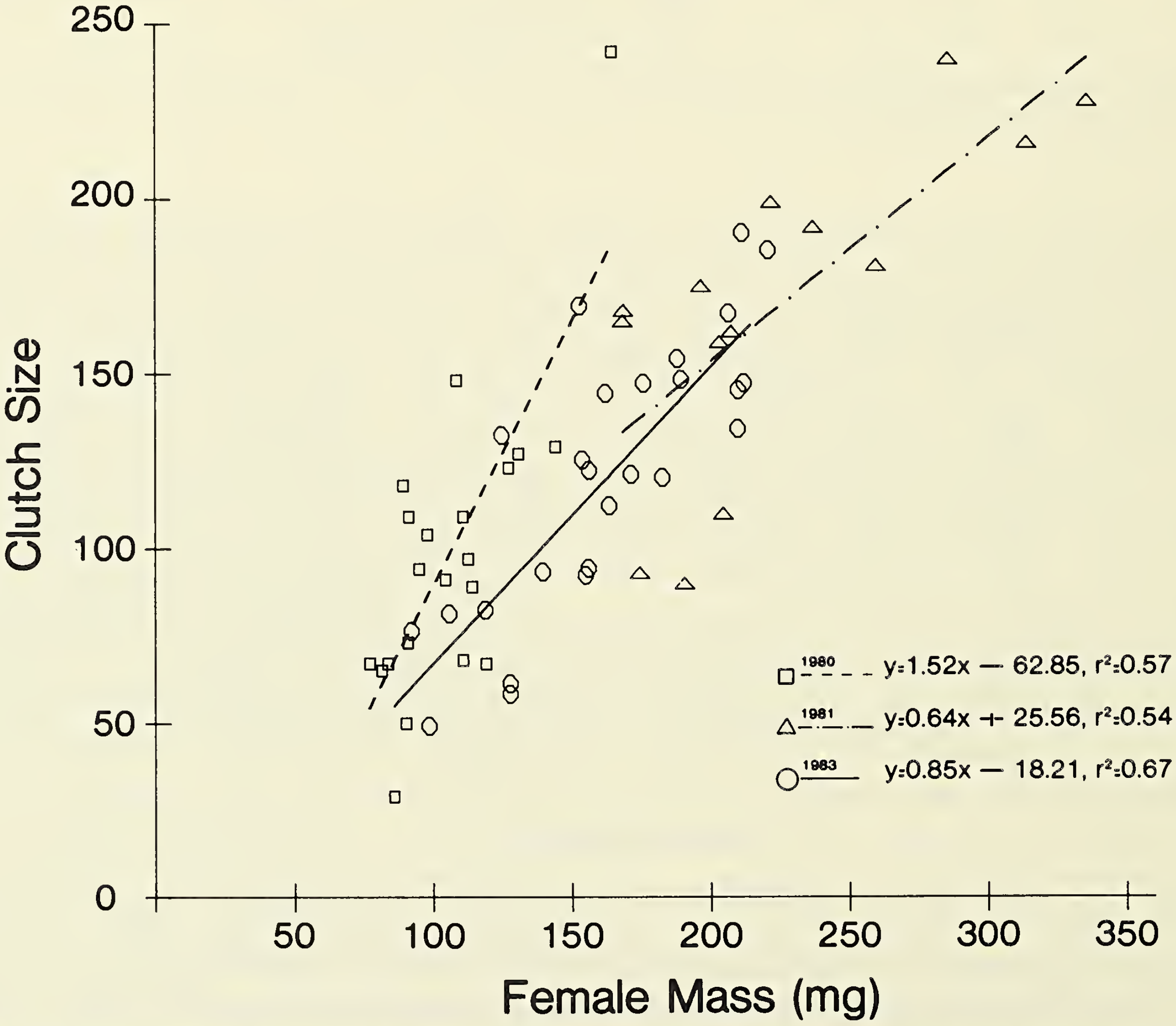

Fig. 2.—Regression of clutch size against female mass of *Peucetia viridans* for three years. r^2 is the coefficient of determination.

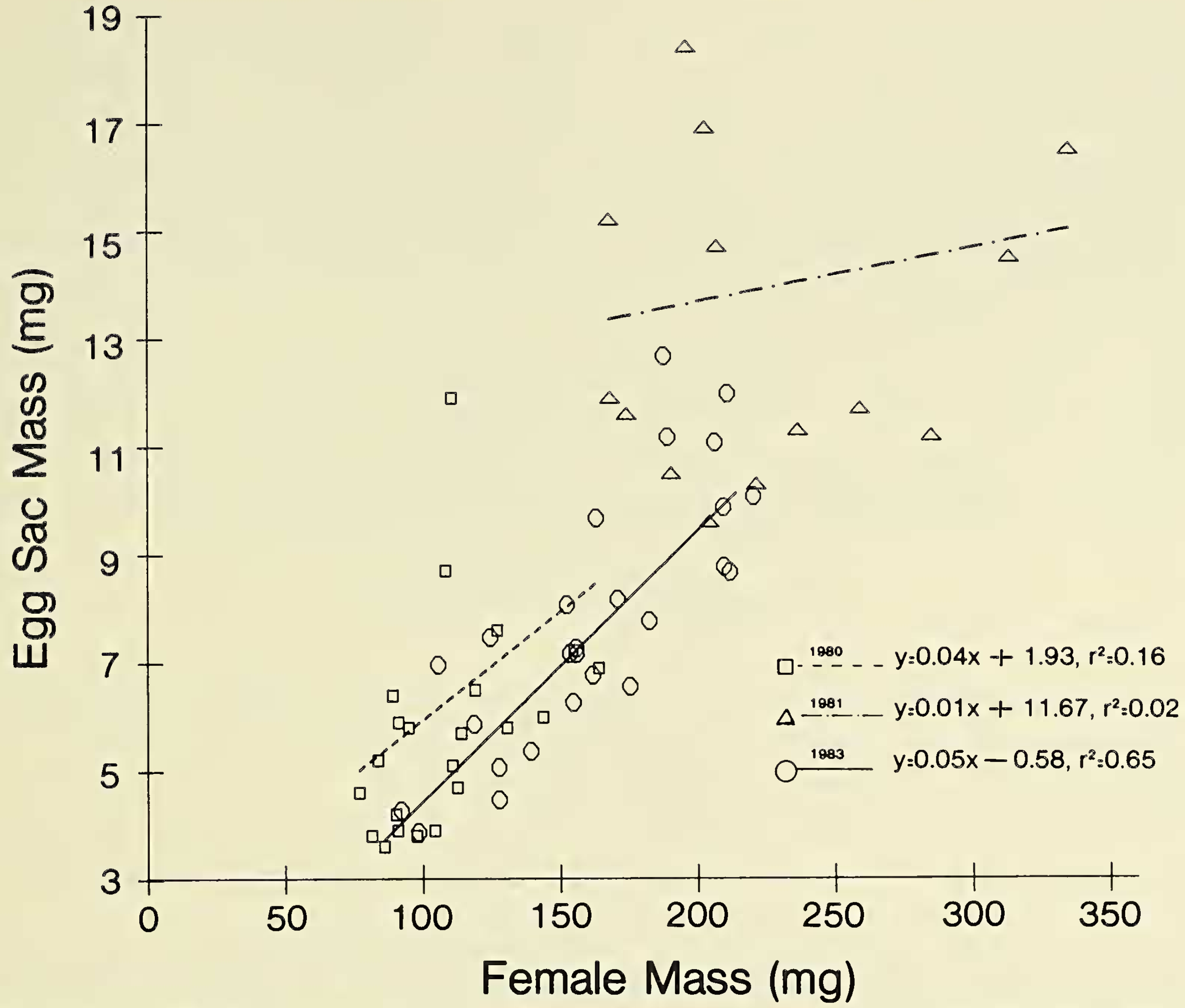

Fig. 3.—Regression of egg sac mass against female mass of *Peucetia viridans* for three years. r^2 is the coefficient of determination.

The larger the female the greater the mass of the egg sac. However, when egg sac mass per young is examined, it can be seen that this parameter has also been optimized by natural selection (Tables 1 and 2). It is obvious that large clutches require more silk for the same degree of protection, but the subtle point is that small females tend to allocate the same amount of energy to egg sac construction per offspring as do large females. Because the construction of an egg sac is a surface to volume related phenomenon, allometric theory predicts the allocation of less silk per young in larger clutches; since egg sac mass per young is constant, egg sacs around larger clutches are likely thicker.

We examine now the broader implications of these life history parameters in this species. Assume that a parameter is a constant from one year to the next if in two of the three years it is not significantly different from the other years. As seen in Table 1, clutch mass, clutch size, mean mass of young, relative clutch mass and egg sac mass per young would be constants. Female size and egg sac mass would therefore be the only variables by year. Under these conditions, it appears that populations of *P. viridans* tend to produce clutch sizes, clutch masses, MMY's, RCM's, and MEY's near optimal values. Female mass and the mass of an egg sac are the parameters left as response variables, able to fluctuate from year to year depending on environmental pressures. We propose the following hypothesis as an explanation for these observations.

Peucetia viridans females protect their offspring in two ways: by watching over the clutch and by covering the clutch with silk. the success of the former protective mechanism depends on the females' endurance after oviposition; the latter mechanism depends on her prey capturing ability before oviposition. For a population to respond favorably to stochastic conditions in the environment (prey and predator presence, temperature, moisture, etc.) some natural history parameters may vary and others may remain constant, depending on the particular selection pressures unique to a species. In *P. viridans* maintenance of successful populations through time requires the tactic of adjusting female size and all the attributes contingent on size. Trade-offs between other parameters may be alternative reproductive tactics in other semelparous species, but in *P. viridans,* female mass and egg sac mass vary in response to environmental pressures to produce adequate numbers of optimal size offspring through optimal reproductive effort, protecting their clutches with optimal egg-sac silk per young.

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